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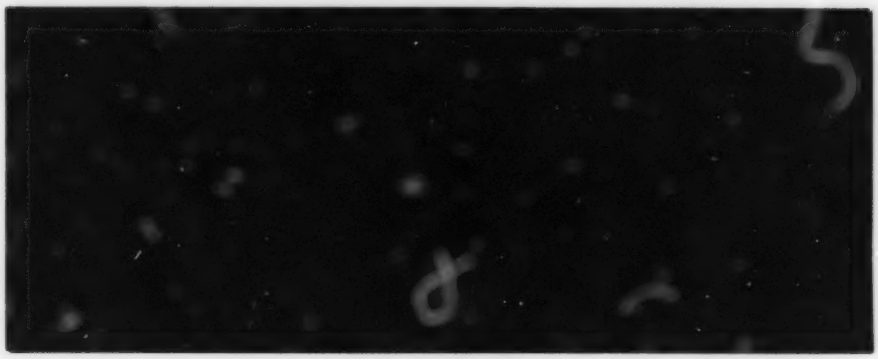

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Technical/Final Report
to
Saskatchewan Agriculture Development Fund

Screening Durum Wheat and Wild Emmer Wheat Germplasm for Drought Tolerance

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EXECUTIVE SUMMARY

(a) **Abstract for agricultural data base:**

The genetic improvement of drought resistance capacity of crop varieties is the only long-term solution of the recurrent drought conditions in Saskatchewan. Toward this goal, an integrated approach was adopted to identify genetic sources of drought resistance in wheat. Because most of the durum wheat acreage in the province is in the drought-prone areas, emphasis was placed on the search for appropriate genetic materials in durum and its immediate wild relative, wild emmer wheat from West Asia. About 5,000 durum and 1,200 wild emmer wheat accessions from diverse origins were evaluated for 28 characters including response to field drought conditions. Fifteen exotic durum and four wild emmer wheat lines were identified as excellent sources of drought resistance. These lines can serve as donor parents for genetic improvements of drought resistance in both durum and hard red spring wheat. Repeated trials with drought-resistant and drought-susceptible durum wheat lines helped to identify two plant attributes, rate of leaf water loss and waxiness of plant surface, which could be used for rapid and reliable screening of wheat genetic materials for drought resistance. Future research on increasing drought resistance in wheat in Saskatchewan will immensely benefit from the results of the research. This research project involved international collaboration and was supported by grants-in-aid of research from the Department of Agriculture, Government of Saskatchewan.

(b) **Summary:**

The grain-growing prairies in western Canada have experienced four (1984, 1985, 1987 and 1988) widespread drought seasons in the past five years. Climatic predictions suggest that the recurrent drought may be a common feature of the agricultural climate on the Canadian prairies in the foreseeable future.

In view of the increasing threat of drought on the Canadian prairies and random changes in weather patterns, it is important to place emphasis on long-term basic research with the goal to develop crop plants tolerant of both gradual and sudden increases in water stress.

Plant tolerance to drought is a complex and composite biological phenomenon. The nature of complexity of this trait dictates that basic research on drought tolerance should be not only multidisciplinary, but also long-term.

There are basically two ways of improving crop production under drought stress: (a) improved field water management and (b) increased genetic resistance of crop plants. The latter offers a relatively long-term solution to the recurrent problem of water stress. For this reason, I initiated a comprehensive research program for identifying genetic sources of drought tolerance in durum wheat, a major cereal crop in western Canada. We adopted an integrated approach, starting with a large scale screening of germplasm lines, which was followed by physiological and biochemical investigations, and then multilocation field verification of selected lines. Our collaborative research involving the University of Saskatchewan, Agriculture Canada Research Station, Swift Current, Saskatchewan and International Centre for Agricultural Research in the Dry Areas (ICARDA), Aleppo, Syria, has clearly demonstrated the value of an integrated approach for increasing crop tolerance to drought

stress. We have developed a drought-tolerant germplasm pool of durum wheat and its immediate wild relative for use in plant breeding, as well as in basic research to elucidate the physiological and genetical basis of drought tolerance in wheat. There has been a worldwide interest in this drought-tolerant germplasm pool.

Although the initial emphasis in our research was placed on durum wheat, our comprehensive strategy for genetic improvement of drought tolerance is applicable also to other major cereal crops in western Canada, such as hard-red spring wheat and barley.

The research project was supported by grants-in-aid of research from the Department of Agriculture, Government of Saskatchewan, Regina, Saskatchewan.

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- Humboldt Journal Article 8 August, 1988.
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- Saskatoon Star-Phoenix Article, 25 July 1988.
- Regina Leader Post Article 25 July 1988.
- Canora Courier Article 10 July 1988.
- Swift Current Sun Article 13 July, 1988.

RADIO BROADCASTS AND OTHER COMMUNICATIONS

- CKOM 650 Radio Saskatoon. Interview with Linda Walker on research and

development on drought tolerance in wheat in Saskatchewan. Three broadcasts on 10 July, 1988.

- CBC Saskatchewan. Three-part series of radio broadcasts on research and development on drought tolerance in wheat in Saskatchewan in the week of 25 July 1988.
- Sixty-three telephone interviews with farmers around the province to explain research and development on drought tolerance in wheat in Saskatchewan, 1 August 1988 - 20 March, 1989.
- Twenty-six letter communications with Saskatchewan farmers on research and development on drought tolerance in wheat in Saskatchewan 10 July 1988 - 20 March, 1989.
- Saskatchewan Research Council News. Drought Research in Saskatchewan. News article. Volume 4, No. 2, July 1988.
- Canadian Press News release. 19 July 1988. Based on a telephone interview with Darlene Rude of Canadian Press, Winnipeg on 18 and 19 July 1988, news and articles on drought research in major Canadian newspapers in July and August, 1988.

TECHNICAL REPORT

TITLE OF PROJECT: **Screening durum wheat and wild emmer wheat germplasm for drought tolerance**

PROJECT LEADER: S. Jana

I. ABSTRACT

Most of the durum and highest quality hard red spring wheat in Saskatchewan are grown in drought-prone areas. Genetic improvement of drought resistance in wheat cultivars is a matter of paramount importance for Saskatchewan Agriculture. The genetic source of drought tolerance for wheat breeding in the province was limited to an introduction from North Africa. Because semi-arid to arid conditions are dominant features of agro-climates in the centre of origin and primary diversity of wheats in West Asia, attempts were made to collect wheat genetic resources from the latter region. A comprehensive evaluation and characterization of about 5,000 durum and 1,200 wild emmer wheat accessions led to the identification of 15 durum and four wild emmer wheat lines that are excellent genetic sources of drought tolerance. These exotic lines substantially broaden the genetic base of wheat breeding materials, and also provide valuable genetic materials for basic research to elucidate the physiological-genetic basis of drought tolerance in wheat. Using drought-tolerant and drought-susceptible groups of durum wheat, significant associations were detected between drought tolerance and five other plant characteristics. These attributes could be utilized singly or jointly for a rapid and reliable screening of wheat germplasm for drought tolerance.

Rigorous field and controlled-environment experiments revealed significant differences between drought susceptible and tolerant genotypes of durum wheat for five physiological parameters. Although these parameters are unsuitable for large-scale field evaluation the results helped to elucidate the physiological basis of drought tolerance in wheat.

A comparative assessment of genetic diversity for 36 isozyme characters in durum wheat and its wild progenitor species from west Asia revealed that wild emmer wheat is a richer source of genetic diversity. However, no consistent pattern of association between plant responses to drought stress and isozymes emerged. Because such biochemical markers would greatly facilitate large-scale screening and selection of drought-resistant genotypes, further research in this area is highly recommended.

II. BACKGROUND AND OBJECTIVES:

Drought is the most important of all environmental constraints that limit crop production in Western Canada. In Saskatchewan alone, an estimated 50% of the wheat-growing land, covering approximately 23% of the arable land, is vulnerable to drought. Severe drought conditions prevailed on a much wider scale in 1984 and 1985, and again in 1987 and 1988 with a devastating impact on cereal crop production. It is well known, however, that drought stress does not have to be of a catastrophic proportion to constitute a serious problem. Short periods of drought during critical periods of crop growth can cause a substantial reduction in crop yield. The genetic modification of crops for better tolerance of both short and long periods of drought and production of economic yields is the only practical solution to the problem.

In view of the Greenhouse Phenomenon, increasing genetic tolerance of crop species to environmental stresses such as drought is of paramount importance in Saskatchewan. For any fruitful work in this area it is important to have at hand a comprehensive collection of germplasm from the areas of great genetic diversity for this trait. For durum wheat and bread wheat, this was partly accomplished through a series of expeditions led by S. Jana since 1978 in the centre of origin and primary centre of diversity of both types of wheats and their wild evolutionary progenitors. During these explorations in Southwest Aisa and eastern Mediterranean countries special efforts were made to collect primitive cultivars (landraces) of durum wheat and diploid, tetraploid

and hexaploid wild wheats from a wide range of environments including extremely harsh environments. Thus, a wealth of genetic resources in both cultivated and wild forms of wheat were available for the proposed research on screening durum wheat and wild emmer wheat germplasm for drought tolerance.

Because of cyclic changes in weather patterns on the prairies, the most realistic and long-term approach toward alleviating the adverse effects of recurrent drought in Saskatchewan is to enhance the genetic adaptation of major Saskatchewan field crops to drought stress, while maintaining high productivity under favourable conditions. However, despite the potential for genetic improvement of drought tolerance in wheat through plant breeding, there has been a paucity of achievements (Richards, 1987). This is mainly because selection and testing for yield and other agronomic characters associated with drought tolerance is slow and expensive, and to a large extent unreliable.

A major problem in breeding for drought tolerance is that the trait is controlled by many genes and significantly modified by the environment (review in Blum 1988). If, however, some physiological, biochemical or morphological markers could be identified that have strong association with drought tolerance, and are relatively little influenced by the prevailing environment then these markers could be conveniently employed in evaluating a large number of germplasm lines for drought tolerance.

The rate of excised-leaf water loss, presumably a measure of cuticular transpiration, was extensively tested in a series of experiments at Swift Current, Saskatchewan as a potential selection

index for drought tolerance in wheat (Clarke and McCaig 1982 a and b, Clarke and Townley-Smith 1986). If additional genetic markers are found, rapid and reliable screening of large numbers of wild and cultivated wheat would be possible. Thus the lengthy, expensive and largely unreliable empirical method of field evaluation of germplasm for drought tolerance could be avoided. The objectives of the research project were formulated with these considerations in mind.

The original overall objective of the research project was to identify genetic sources of drought tolerance, which could be used in improving drought tolerance of durum wheat cultivars grown in Saskatchewan. The specific objectives were threefold:

1. Evaluation and characterization of durum wheat and its immediate evolutionary progenitor, wild emmer wheat, collected from their centre of origin and diversity in West Asia and eastern Mediterranean countries.
2. Identification of drought tolerant exotic durum wheat and wild emmer lines that are adapted to Saskatchewan field drought conditions.
3. Identification of biochemical and physiological markers (traits) that can be used to reliably screen wheat germplasm for drought tolerance.

There was no deviation from the original objectives.

III. EXPERIMENTAL METHODS

(a) Germplasm evaluation:

As a part of the crop genetic resources collection and conservation programme at the University of Saskatchewan, about 12,000

accessions of durum wheat (**Triticum turgidum** var **durum**) and 1,200 wild emmer wheat (**T. turgidum** var. **dicoccoides**) were assembled from diverse sources throughout the world. A major source of these materials was the centre of origin and primary centre of diversity of the two species in the Near East Fertile Crescent.

About 5,000 durum wheat and 1,200 wild emmer wheat accessions were grown in Saskatoon in 1985 (annual precipitation 330 mm and growing season rainfall 159 mm). Each accession was grown in a single 5 m-row plot interspersed with local check cultivars, Pelissier, Wakooma, Hercules and Kyle, at regular intervals. These accessions were characterized for 28 characters (Table 1). These characters included both categorical and continuous measurement variables. All accessions were evaluated for overall agronomic performance under field drought conditions using an ordinal scale of 1 (poor) to 9 (excellent).

The durum wheat and wild emmer wheat accessions were grown in single-replicate plots Swift Current in 1985, and 1988, respectively, and the rate of excised-leaf water loss and leaf water retention capacity were measured during the vegetative growth phase using a semi-automated technique described by McCaig (1986).

Additional field evaluation of the 5,000 durum wheat accessions was carried out in 1985-86 at an arid location (Breda, 35°56'N and 37°10'E, elevation 300 m, annual precipitation 300 mm and growing season rainfall 218 mm) in northern Syria. The 1200 wild emmer wheat accessions were evaluated at an arid site in northern Syria (Breda) for drought tolerance in two seasons, 1986-87 and 1987-88.

Statistical analyses: Preliminary data analyses were performed using

the product-moment correlation and contingency chi-square tests for exploring bivariate associations. These analyses were followed by multivariate statistical analyses of data to determine multicharacter associations. The BMDP multivariate programmes were used on a VAX 8650 computer at the University of Saskatchewan:

Nature of dependent variables	Nature of independent variables	Multivariate statistical methods used	BMDP Program used
Continuous	Continuous	Multivariate multiple regression and canonical correlation	6R and 6M
Categorical	Categorical	Log-linear analysis	4F
Categorical	Continuous	Discriminant analysis	7M
Continuous	Categorical	Multivariate analysis of variance (MANOVA) and analysis of covariance (ANCOVA)	4V

In addition to the above multivariate procedure, Shannon's information statistics and polymorphic indices were calculated for a comparative assessment of genetic diversity in wild and cultivated wheats as outlined by Jana and Pietrzak (1988).

(b) Identification of elite lines using physiological criteria:

Plant responses to moisture stress using physiological criteria have been studied extensively (see Blum 1988 for a review). Despite the possibility of precise and accurate measurement, most of these parameters are not applicable to large-scale screening of crop germplasm. Of several drought-adaptive physiological traits, rate of excised-leaf water loss (RWL) and excised-leaf water retention capacity (RWC) has shown promise as an effective physiological criterion related

to yield potential under drought (Clarke, 1987 and earlier). The usefulness of this method in practical terms was extensively studied at the Agriculture Canada Research Station, Swift Current, Canada. The method presumably measures the rate of cuticular transpiration from young fully turgid leaves, although leakage through incompletely closed stomata cannot be completely ruled out. About 5,000 durum and 1,200 wild emmer wheat accessions were evaluated for RWL using the semi-automated method described by McCaig (1986). On the basis of this evaluation, 50 genotypes with the lowest and 50 genotypes with the highest RWL were identified without regard for any other traits. These genotypes, together with local checks were subsequently used for detailed studies on their responses to drought stress. Fifteen durum wheat and four wild emmer wheat genotypes were also found to be well-adapted to Saskatchewan conditions and potentially valuable donor parents for drought tolerance.

(c) Field studies on physiological parameters:

Sixteen durum wheat accessions were chosen for this study, eight from the low-RWL group of 50 and another eight from the high-RWL group of 50 genotypes. Two relatively drought-tolerant Canadian cultivars (Pelissier and Wakooma) and two drought-susceptible Canadian cultivars (Hercules and Kyle) were also included in a field study (a) to determine differences in grain yield and nine physiological characters, and (b) to examine associations of these characters with drought tolerance. Because previous Canadian research showed significant correlation between the rate of excised-leaf water retention capacity and drought tolerance, (Clarke and McCaig, 1982a and later), the RWL-data were used

to classify the 20 genotypes into the two groups of 10 drought-tolerant and 10 drought-susceptible genotypes. These 20 genotypes were grown in Saskatoon in a field experiment in a randomized complete block design with four replications under both irrigated and dryland conditions in a favourable year (1986, growing season precipitation = 252.2 mm, 50-year average = 190.8 mm) and a dry year (1987, growing season precipitation = 126.2 mm).

Soil was of the chernozemic, orthic dark brown subgroup (Typic Haploborall) and was of the Bradwell association consisting of fine sandy glaciolacustine deposits (Acton and Ellis 1978). Each genotype was planted as a 75 cm row within each block and separated from the next genotype by two rows of winter wheat, cv. Norstar, planted 30 cm apart. Seeds were pretreated with Vitavax fungicide (Uniroyal Chem., Ontario, Canada) and planted at a seed rate of 50 seeds per row. Planting dates were 1 May, 1986, and 28 April, 1987, for the non-irrigated field treatment and 3 May, 1986, and 4 May, 1987 for the irrigated field treatment. Approximately 20 mm of irrigation water was applied weekly by a wheelmove sprinkler system while the non-irrigated field received natural precipitation only (May to harvest precipitation = 246.1 mm 1986, 12.5 mm 1987). No fertilizer was applied in either 1986 or 1987 as soil tests showed the nutrient level to be adequate.

In each year, approximately four weeks after planting, the most vigorous plant in each genotype row in each block was visually identified and tagged. Physiological characters were measured starting four weeks after planting. Measurements were made once a week for seven weeks in 1986 and for six weeks in 1987 on the most recent, fully

expanded leaf on the main tiller of the tagged plant for the following nine physiological characters: photosynthetic CO_2 exchange rate (CER; μmol $m^{-2}s^{-1}$), stomatal resistance (r_s; s cm^{-1}), internal CO_2 concentration (INCO2; ppm), water-use efficiency (WUE; μmol $mmol^{-1}$), chlorophyll a+b content (Chl; μg cm^{-2}), specific leaf weight (SLW; g cm^{-2}), rate of excised-leaf water loss (RWL; %), leaf water content (LWC; %) and total leaf area (LA; cm^{-2}).

CER, r_s, internal CO_2 concentration and initial transpiration rates were measured with the LI-COR 6000 Portable Photosynthesis System (LI-COR Inc., Lincoln, Nebraska). Transient WUE was calculated as the ratio of CER and initial transpiration rate. Chl was measured according to the method described by Hobbs and Mahon (1985).

SLW was determined on random samples from each plot of five of the most recent, fully expanded leaves on the main tiller of untagged plants. Their leaf area was measured with a LI-COR area meter (LI-COR Inc., Lincoln, Nebraska) and their dry weight was determined after 36 h at 70°C.

LI-COR measurements were made on all tagged plants in random order within a block in a treatment between 0830 and 1230 hours to ensure that measurements were most often made under cloudless conditions. Leaf discs for Chl determinations were collected from the same plants between 1330 and 1500 hrs. Therefore, plants in the irrigated and non-irrigated treatments each required a day to sample and the order in which the treatments were measured in any one week was randomized. Specific leaf weight (SLW) was measured four times during both 1986 and 1987. Once each year, one mid-season measurement was made for leaf area on a single

untagged plant in each genotype row for two blocks in 1986 and all four blocks in 1987.

For soil moisture determination, soil samples to a depth of 50-75 cm (from each plot in each treatment) were obtained using an auger. Percentage of soil moisture was expressed as ((initial weight - oven-dried (70°C) weight)/oven-dried weight) x 100. Days to heading was calculated as the number of days from planting to the day at which 50% of the heads fully emerged from the flag leaves. The number of days from planting to complete senescence of the plants were taken as days to maturity. Plant glaucousness was determined using the scoring method described by Fisher and Wood (1979) with a slight modification. Instead of a scoring method of 1-3, waxiness was scored on a 1-9 scale (with 1 indicating maximum waxiness and 9 indicating poor waxiness of the leaves). At maturity the tagged plant in each row was harvested at ground level, air-dried at room temperature for a week and above-ground biomass, (shoot dry weight) and grain yield were determined.

Statistical analyses: A nested analysis of variance was carried out for each character separately for each year with irrigation treatments as main treatment, genotypes as sub-treatments and measurement days (age) as sub-sub treatments. Significant genotype effect was separated further into tolerant versus susceptible group effect and was tested against the within group effect. An appropriate transformation (Y = Log X + 1) was used for shoot dry weight and yield to remove heterogeneity of error variances between the irrigated and dryland experiments in each year and a combined analysis of variance was calculated. Within each year, linear correlation coefficients between different characters were

estimated by using the overall genotype means.

(d) Controlled-environment experiments on physiological parameters:

Two independent experiments were conducted in controlled-environment chambers to study the effect of water stress and subsequent relief from stress on six physiological characters: photosynthetic CO_2 exchange rate (CER), stomatal resistance (r_s), internal CO_2 concentration (INCO2), water-use efficiency (WUE) chlorophyll a+b content (Chl) and transpiration rate.

In the first experiment, nine drought-tolerance (low-RWL) and 10 drought-susceptible (high-RWL) durum wheat lines were used. Three seeds of each genotype were sown in six-inch pots filled with Turface (AMCOR, Deersfield, IL.) potting soil, treated with Nutricote (Chisso-Asahi Co. Ltd. Ontario, Canada) controlled release fertilizer and watered daily. Pots were arranged in a randomized complete block design with five replicates. Plants were grown at 20°C/15°C day/night temperature with a 16 hour photoperiod. Light was supplied with mixed Metallarc/Lumalux lamps at an intensity of 800-850 $\mu E\ m^{-2}\ s1$. One week after emergence, the seedlings were thinned to one per pot. Measurements were recorded on CO_2 exchange rate (CER), stomatal resistance (r_s), water-use efficiency (WUE), internal CO_2 concentration (INCO2), and chlorophyll content (Chl) as previously described in Section C. Transpiration rate was also measured by a LI-COR 6000 portable photosynthesis system (LI-COR Inc., Lincoln, Nebraska).

Plants were watered daily until 40 days after planting (no-stress period). Daily watering was then stopped until 54 days (stress period) when it was resumed until the end of the experiment at 64 days

(rewatering period). Plants received 100 ml of water each on 46 days to prevent development of fatal stress conditions. Measurements were made on: 28 and 35 days (no stress); 42 and 49 days (stress); 56 and 63 days after planting (rewatering).

Statistical analyses: All characters except for WUE exhibited heterogeneity of the error variances among the three treatments. Therefore, an analysis of variance was performed separately under each treatment condition. Genotype differences within each treatment were separated into the tolerant and susceptible group effect, which was tested against the within group effect. Correlations among characters were calculated using overall genotype means within the stress and rewatering treatments.

In the second experiment, eight genotypes, 4 tolerance and 4 susceptible, exhibiting responses typical of their respective groups during the stress and rewatering periods in the first experiment were selected to study the immediate effects of changing water regime on plant physiological characters. Three seeds of a genotype were planted per pot and the pots were arranged in a randomized complete block design with five blocks. Growing conditions of the plants were similar to those described for the first experiment. One week after shoot emergence, plants were thinned to one plant per pot.

Measurements were recorded for all characters on each plant 20 days after planting (no stress) as described for the first experiment. Stress (withdrawal of watering) was introduced on 26 days after planting and similar physiological measurements were made daily from 27 to 32 days and on 35 days after planting (stress). Prior to initiation of

stress, pots were covered with plastic wrap to minimize water loss from the surface of the potting soil. Watering was resumed on 35 days after planting and measurements were made from 36 to 39 days, which constituted the rewatering treatment.

(e) Multilocation field experiments:

As mentioned earlier, rate of water loss from excised wheat leaves (RWL), a measure of cutivular transpiration, has been successfully used by Canadian researchers to identify wheat genotypes for dry environments (Clarke and Townley-Smith, 1986). Because some low-RWL genotypes had poorer yield than high-RWL genotypes under favourable field moisture conditions, it was important to know whether there was a metabolic carbon cost associated with low RWL in favourable environments. To clarify this possibility an experiment was conducted with several durum wheat genotypes of diverse origins in a range of environments (Clarke et al., 1989). The 50 lowest RWL and the 50 highest RWL genotypes (see Section b above) were selected on the basis of their rates of water loss from excised leaves.

Statistical analyses: Analysis of variance and product-moment correlation between characters were carried as described for the first experiment. These 100 genotypes together with four Canadian cultivars (Medora, Pelissier, Wascana and Wakooma) were grown in replicated trials without irrigation in Swift Current (1985 and 1986), and Saskatoon (1985, 1986 and 1987) in Canada, and in one semi-arid (Tel Hadya) and two arid (Breda and Bouilder) locations in northern Syria in the 1985-86 growing season. In addition, a replicated field trial involving these 104 genotypes was conducted in Saskatoon in 1986 under irrigation.

Environmental data and location mean yields suggested the following increasing order (no stress to most severe) of drought-stress conditions that prevailed at the nine experimental sites: Saskatoon (irrigated), Tel Hadya, Saskatoon (non-irrigated) 1986, Swift Current 1986, Saskatoon 1985, Saskatoon 1987, Breda, Swift Current 1985, and Bouider.

Heading date, maturity date, and grain yield data were collected at all locations. Glaucousness was scored visually at Swift Current in 1985 and Breda using a score of 1 for highly glaucous, 5 for moderately glaucous, and 9 for low or non-glaucous. Excised-leaf water loss rates were measured at Swift Current in 1985 and 1986.

Statistical analyses: The diverse nature of the genotypes, particularly with regard to days to heading and maturity made it necessary to remove some genotypes from the analyses. Genotypes with heading dates in the range $\pm$ 3 days of the checks in the Canadian studies and $\pm$ 5 days in the Syrian studies were used in the final analyses of yield performance. The maturity range corresponded to approximately $\pm$ 2 standard deviations from the checks. This avoided confounding RWL with drought avoidance through rapid phenological development. The number of genotypes remaining for comparison within sites ranged from 49 to 75.

Comparison of the yields of the low and high RWL and low (ratings 1 and 5) and high (rating 9) glaucousness genotypes was made in two ways. Average yields of the high and low groups were compared by analysis of variance. Within the range of heading dates chosen, yields were adjusted by covariance on heading date where statistically appropriate. A combined analysis across locations and years was not possible due to differing entries and experimental designs. The second

procedure compared the relative frequencies of low RWL and high glaucousness genotypes in the whole data set and in the top yield quartile within each location. This provided a measure of the randomness of the distribution of low vs. high genotypes for yield, and was statistically evaluated by the hypergeometric probability distribution (Steel and Torrie, 1980).

(f) Electrophoretic study:

The purpose of this study was to identify some biochemical markers for drought tolerance, and for one or more physiological traits that are associated with drought tolerance. Because earlier studies at Swift Current and Saskatoon revealed significant association between excised-leaf water retention capacity and drought tolerance in durum wheat, we used 100 durum wheat lines with known excised-leaf water retention capacity in the first phase of the study. Laboratory procedures were standardized for horizontal starch-gel electrophoresis for 36 isozymes systems listed in Table 2. Genetic diversity for isozymes was assessed in both wild emmer and durum wheat using the procedures described by Jana and Pietrzak (1988).

IV. RESULTS AND DISCUSSION

(a) Germplasm evaluation

Multivariate analyses of continuous and categorical data collected from the evaluation nurseries in Swift Current and Saskatoon revealed significant associations of four characters, seedling vigour, glaucousness of plants, plant height and maturity period with overall agronomic score under dryland conditions. Further, evaluation of the

5,000 durum accessions at a highly arid location (Breda, 35°56N, 37°20'E, annual rainfall, 279 mm) in northern Syria in the 1985-86 season confirmed the Saskatoon results. These results suggest that an integrated selection index involving these multiple traits is the most reasonable approach toward identifying drought-tolerant durum wheat genotypes for breeding purposes. Additional research is in progress both at the University of Saskatchewan, Saskatoon, Canada and International Center for Agricultural Research in the Dry Areas Aleppo, Syria to develop an efficient selection index for genetic improvement of drought tolerance in durum wheat, as well as in bread wheat and barley.

(b) Identification of elite germplasm using physiological criteria:

Durum and wild emmer wheat accessions were evaluated for the rate of water loss from excised leaves (RWL) at Swift Current. On the basis of this evaluation, 50 durum wheat genotypes with the lowest and 50 genotypes with the highest RWL were identified without regard for any other traits. These genotypes, together with local checks were subsequently used for detailed studies on their responses to drought stress in multilocation field locations. Some of the durum wheat lines were also used for detailed studies to elucidate physiological basis of drought tolerance in wheat. A series of field and controlled-environment studies on agronomic and physiological criteria confirmed drought tolerance potential of the selected lines. Fifteen durum wheat and four wild emmer wheat genotypes were also found to be well-adapted to Sakatchewan conditions and potentially valuable donor parents for drought tolerance.

(c) Field studies on physioslogical parameters:

Mean RWL and LWC measurements under both irrigated and non-irrigated conditions confirmed the earlier classification of the 20 durum wheat lines into the two groups of 10 low-RWL and 10 high-RWL genotypes. The low-RWL genotypes were more glaucous and later in maturity under both experimental conditions. However, for grain yield, INCO2, WUE, Chl, SDW and LA, the differences between the groups were significant only under non-irrigated conditions (Table 3). The lack of significant difference in grain yield between the groups under irrigation provided additional evidence that the low-RWL genotypes were truly drought tolerant, rather than those with high yield potential under both favourable and unfavourable moisture conditions. There were no significant ($P = 0.05$) differences between the two groups for CER, r_s, and SLW under either condition. Pearson's product-moment correlation coefficients showed consistent association of RWL with INCO2, Chl, LWC, SDW and grain yield per plant (Table 4). The strong correlation between RWL and LWC indicated that either RWL or LWC could be used as a useful physiological criterion in screening durum wheat germplasm for drought tolerance. The method of measuring the rate of leaf water loss from excised leaves has been automated at the University of Saskatchewan, Saskatoon and at Agriculture Canada Research Station, permitting rapid and reliable evaluation of large numbers of wheat genotypes.

Significant differences between genotype means, averaged over measuring days and irrigation treatments within each year, were evident for all characters except leaf area in 1986 (Table 3). Only shoot dry

weight showed a significant overall genotype x irrigation interaction suggesting that genotype ranking for other characters was stable with a change in water availability. Genotype rankings between years were also generally consistent as indicated by the positive correlations observed between the genotype means in the two years (Table 4), although r_s, leaf area and yield were not significant. Such consistent variability is highly beneficial if selection for improvement of these characters is to be carried out.

Weather conditions were markedly different between the 1986 and 1987 growing seasons. Saskatoon was particularly dry in 1987 and recorded only 53% of normal precipitation from May - July, while in 1986 above normal precipitation (144%) was recorded during the same period. In addition, high net evaporation rates (Means: 1986 = 220 mm, 1987 = 234 mm, 50 year average = 218 mm) and mean maximum temperatures (Means: 198 = 21.8°C, 1987 = 24.1°C, 50 year average = 21.8°C) led to a larger evaporative demand on the plants creating a greater degree of water stress in 1987 than in 1986. Soil moisture determinations indicated a lower average water content in the non-irrigated (Means: 1986 = 17.1%, 1987 = 15.9%) than in the irrigated treatment (Means: 1986 = 26.2%, 1987 = 26.6%).

Significant differences between non-irrigated and irrigated treatment means were evident in both years for CER, r_s, leaf area, yield and shoot dry weight, but only in 1987 for internal CO_2 concentration (Table 3). Under non-irrigated conditions, there were significant differences between the tolerant and the susceptible groups for internal CO_2 concentration, WUE, Chl, leaf area, shoot dry weight and yield. The

greater Chl of the tolerant genotypes might increase their photosynthesis under low-light conditions (Stout and Simpson 1977) and also increase their WUE (Johnson et al. 1983). Although, the tolerant and susceptible genotypes did not differ significantly for CER, the tolerant genotypes had a significantly lower internal CO_2 concentration of the tolerant genotypes, as compared to the susceptible genotypes, under similar stomatal resistance might be due to an efficient CO_2 depletion or fixation rate (Farquhar and Richards 1984). WUE was higher in the tolerant genotypes under non-irrigated conditions. Although WUE was measured under transient conditions in the studies, higher WUE has been related to higher drought tolerance by Morgan and Condon (1986).

The tolerant genotypes had a higher number of days to heading (tolerant = 61, susceptible = 56 in 1986; tolerant = 57, susceptible = 51 in 1987) and a higher number of days to maturity (tolerant = 107, susceptible = 101 in 1986; tolerant = 100, susceptible = 94 in 1987) than the susceptible genotypes. Leaves of the tolerant genotypes may have contributed extra days of carbon-gain during the critical grain-filling period. The presence of a greater amount of wax on leaf surfaces of the tolerant genotypes (Tolerant = 1, Susceptible = 5) could have delayed leaf senescence by reducing leaf temperature or helped to maintain a favourable water status.

Higher yields of the tolerant genotypes could not be explained by CER differences between the tolerant and susceptible genotypes (Table 4). However, under non-irrigated conditions in 1987, there was an apparent relationship between flag leaf CER and yield as indicated by a significant correlation between these two characters ($r = 0.81$, $p <$

0.01). Correlations between genotype means of flag leaf CER and yield during 1986 (in non-irrigated, $r = 0.31$, $p > 0.05$: in irrigated, $r = 0.13$, $p > 0.05$) and under irrigated field conditions in 1987 ($r = 0.35$, $p > 0.05$) were not significant. It has been suggested that, under mild to moderate stress conditions, lower leaves make a greater contribution to grain-filling, but under moderate to severe stress conditions (non-irrigated 1987) grain-production depends entirely on photosynthetic structures above the flag leaf node area (Simpson 1968, Kaul 1974). Thus the exploitation of genetic variation in flag leaf CER under such stress conditions might be for enhancing tolerance in wheat.

Photosynthetic capacity is determined by total leaf area as well as photosynthesis per unit area. The tolerant genotypes had a higher leaf area than the susceptible genotypes under non-irrigated field conditions (Table 3). This could lead to higher canopy photosynthetic rates for the tolerant genotypes than the susceptible genotypes. Plants that maintain a higher green leaf area could tolerate dehydration while maintaining high water potentials and should be selected under dry conditions.

Consistent genotypic differences were evident for physiological characters in 20 durum wheat genotypes tested under markedly different environmental conditions. Drought tolerance was related to several other characters. The tolerant and susceptible genotype means differed significantly for internal CO_2 concentration, WUE, leaf area, Chl and shoot dry weight but only under conditions of greater water stress. These results indicate that these characters can be used under moisture-stress conditions to identify potentially drought-tolerant wheat

genotypes.

(d) Controlled-environment experiments on physiological parameters:

Two independent experiments in contolled-environment chambers were conducted involving drought-tolerant and drought-susceptible genotypes experiments in each experiment. The purpose of these was to study the physiological responses of drought-tolerant and drought-susceptible durum wheat genotypes under water stress, and during recovery from water stress. Of the six physiological characters studied, r_s increased during the stress period in both groups of genotypes in both experiments (Fig. 1). Subsequent rewatering caused r_s to return to pre-stress levels. WUE also increased during stress and decreased on rewatering, but did not return to pre-stress levels. All other characters decreased with the induction of drought stress and recovered partly upon rewatering. The tolerant genotypes showed a higher level of recovery of CER and Chl than the susceptible genotypes most likely because they maintained a higher water potential. This might have provided a greater protection against chlorophyll destruction under stress and allowed greater recovery on rewatering.

As described in the previous section, the tolerant and susceptible genotypes differed significantly for Chl, WUE, and internal CO_2 concentration in addition to leaf area, shoot dry weight and yield under field conditions. Under controlled coinditions the group differences for Chl, internal CO_2 concentration and WUE were evident, but for the latter two characters only after the plants had undergone a stress cycle, perhaps because 'prestressed leaves' behave like 'field leaves' (McCree 1974). The group differences for CER and r_s were observed only

under controlled stress conditions. Failure to observe such differences for CER and r_s under field conditions could be due to (a) group difference for these characters being evident only under severe stress conditions, not encountered in the field, or (b) the group difference being present in the field, but not in the morning when the characters were measured.

(e) Multilocation field experiments:

Grain yields of respective genotypes were measured at each site, and pooled to obtain mean yields of the two groups, low-RWL and high-RWL (Table 5). The low-RWL genotypes yielded more than the high-RWL genotypes in four of the five drier sites, Bouider, Swift Current 1985, Saskatoon 1987 and 1985. Despite higher mean yield of the low-RWL group, the difference between the groups was not significant at Breda. There was no indication of a yield disadvantage of the low-RWL genotypes in the favourable sites, Saskatoon (irrigated), Tel Hadya, Saskatoon (non-irrigated) and Swift Current 1986. The results support the earlier observations of Clarke and Townley-Smith (1986) that the yield advantage of the low-RWL genotypes in dry environments is not associated with any detectable metabolic cost in moist environments. Thus incorporating high leaf water retention capacity into commercial varieties should increase yield potential in drier environments without limiting their yield potential in moist environments. Most of the low-RWL genotypes used in this study were also more glaucous than the high-RWL genotypes, making it impossible to separate the effects of glaucousness and RWL on grain yield. However, in a separate field experiment involving 79 non-glaucous wheat genotypes conducted at Swift Current in 1985, low-RWL

genotypes yielded significantly higher than high-RWL genotypes (Agriculture Canada Research Station, Swift Current, unpublished research data). Under severe moisture-limiting conditions, both glaucousness and low RWL are found to be beneficial to the wheat plant. While high level of epicuticular wax (glaucousness) lowers leaf temperature and stomatal conductance (Richards et al. 1986), low RWL promotes water conservation during periods of stomatal closure (Rawson and Clarke, 1989). Our multilocation experiment indicates that both glaucousness and RWL are associated with drought response in wheat, and both serve as reliable markers for drought tolerance in a wide range of soil moisture conditions in the long-day temperate climate of western Canada, as well as short-day Mediterranean climate of northern Syria.

(f) Electrophoretic study:

In the past five years, several geneticists have successfully used isozyme loci as genetic markers for quantitatively inherited characters (Kahler and Wehrhann, 1986; Edwards et al. 1987; Stuber et al. 1987). Recent work on rice at the International Rice Research Institute, Manila, Phillipines has shown that some esterase isozyme markers can be used effectively for screening large numbers of rice germplasm lines for freezing stress tolerance. We studied genetic variation in 1,200 wild emmer wheat and an equal number of durum wheat accessions for polymorphism for 36 isozyme systems. Durum wheat showed polymorphisms for 22 of the 36 isozymes studied. These are: Acp-1, Acp-2, Acp-3, Aco-1, Aco-2, Dia-1, Dia-2, Enp-1, Est-1, Est-2, Est-3, Est-4, G-6Pd-1, 6-GPd-2, Lap-1, Me, Per-1, Per-2, Pgi-1, Pgi-2, Pgd-1 and Pgd-2. In wild emmer wheat, variants were found for 31 of the isozymes, suggesting

that wild emmer population accessions of the Near East Fertile Crescent are genetically more variable than the cultivated durum landrace populations of the region. A comparative assessment of genetic diversity in wild emmer and durum wheat accessions from West Asia using Shannon's information statistics and polymorphic indices confirmed the conclusion (Table 6).

Thus wild emmer wheat of the Fertile Crescent in West Asia appeared to be a rich source of genetic diversity which could be utilized in both durum and bread wheat improvement. The natural distribution of this species in the region extends from very favourable to very harsh environments characterized by low soil moisture and high temperature conditions during the major part of the growing season. These populations of this species has been found to harbour substantial genetic variability for many useful attributes, such as adaptation to arid conditions, low and high temperature, and seed protein content (Nevo 1983; Nevo et al. 1988). The isozymes studied during the tenure of the project most probably represent a random sample of gene loci from the entire AABB genome of wheat, many of which are almost certainly linked with many desirable plantattributes including drought tolerance. The comprehensive results of our studies on agronomic, morphological, physiological and biochemical characters reveal the importance of wild emmer wheat accessions in broadening the genetic base of breeding materials for wheat improvement in Saskatchewan. Although our studies so far revealed no statistically significant association of one or more of the biochemical markers with plant response to drought stress, in view of the encouraging results in corn and rice, the search for genetic

linkage of isozyme markers with drought tolerance holds high promise, and warrants concerted future efforts.

V. CONCLUSION AND IMPACT

The grain-growing prairies in western Canada have experienced four (1984, 1985, 1987 and 1988) wide-spread drought seasons in the past five years. Climatic predictions suggest that recurrent drought may be a common feature of the agricultural climate on the Canadian prairies in the foreseeable future. The increasing frequency and severity of drought conditions in large parts of the province amply demonstrate that our research and development in drought resistance in wheat was timely and appropriate.

There are basically two ways of improving crop production under drought stress: (a) improved field water management and (b) increased genetic resistance of crop plants. The latter offers a relatively long-term solution to the recurrent problem of water stress. We recognized that an integrated approach, starting with a large scale screening of germplasm lines to the utilization of promising genetic resources through conventional breeding, cytogenetic manipulation and molecular genetic technique would be an appropriate strategy. Although the initial emphasis was placed on durum wheat, our comprehensive strategy for genetic improvement of drought tolerance is applicable also to other major cereal crops in western Canada, such as hard red spring wheat and barley.

Genetic diversity is the raw material for any plant breeding. The Near East Fertile Crescent is the original home of diversity of both durum and bread wheats and their wild evolutionary progenitors. The region abounds in genetic diversity in both cultivated and wild forms of wheat. Agro-climatic conditions in much of the Fertile Crescent are

dominated by frequent drought and temperature stresses. For this reason, we carried out an extensive survey of wild and cultivated landrace populations of wheat collected from this region. Our survey revealed that excellent sources of drought tolerance exist in sufficiently high frequencies (1-2 percent) in many of these exotic populations of wild and primitive cultivated wheat.

Our studies also indicated that using appropriate phenological, morphological and physiological parameters, it is possible to identify true-breeding drought-tolerant lines in a relatively short period of three years. Multilocation field experimentation under moisture-stress conditions and assessment of the rate of water-loss from excised leaves of growing plants enabled us to identify 50 durum wheat and 12 wild emmer wheat lines that were highly drought tolerant. Further investigation of these lines for agronomic performance in Saskatoon and Swift Current led to the identification of 15 durum wheat and 4 wild emmer wheat lines that are well-adapted to Saskatchewan growing conditions. Thus, we have at hand not only several thousand durum and wild emmer wheat accessions, which provide genetic diversity for a large array of characters, but also a number of "proven" genetic materials. These genetic resources can be utilized in conventional plant breeding, as well as in time-saving modern genetic engineering tehcnologies for improving dorught resistance in wheat. As the present studies indicated, these are also very valuable experimental materials for basic research in genetics and whole-plant physiology to elucidate the basic mechanisms of drought resistance in wheat.

Crop response to drought stress is a complex character. In the

present studies, this complexity was further complicated by substantial genotype-environment interaction. Using multivariate statistical procedures to elucidate complex multi-character associations, we were able to identify a group of plant attributes that showed consistent associations with drought stress. This discovery is significant because it makes indirect selection for drought tolerance possible and relieves the plant breeder of the enormous task of large-scale field testing of segregating generations from planned hybridization.

ACKNOWLEDGEMENT: The research reported here was suppported by grants-in-aid of research from the Department of Agriculture, Government of Saskatchewan, Regina, Saskatchewan.

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Table 1. The list of 28 characters used for evaluation and characterization of durum and wild emmer wheat germplasm.

Type of Character	Character	Type of observation recorded*
Phenological	Days to flowering	Measurement
	Days to maturity	Measurement
	Grain-filling period	Measurement
Physiological	Early vigour	Categorical (3)
	Growth class	Categorical (3)
	Leaf rolling	Categorical (2)
	Overall agronomic performance	Categorical (9)
	Grain yield	Measurement
	Kernel size	Measurement
	Rate of leaf water loss	Measurement
	Leaf-water retention capacity	Measurement
Morphological	Juvenile growth habit	Categorical (3)
	Waxiness of plant	Categorical (3)
	Flag-leaf attitude	Categorical (3)
	Flag-leaf length	Measurement
	Flag-leaf width	Measurement
	Awnedness	Categorical (3)
	Awn colour	Categorical (3)
	Spike density	Categorical (5)
	Spike length	Measurement
	Number of seeds per spike	Measurement
	Glume hairiness	Categorical (3)
	Glume colour	Categorical (5)
	Plant height	Measurement
	Productive tillering capacity	Categorical (3)
	Straw strength	Categorical (3)
	Stem solidness	Categorical (2)

*Numbers within parentheses represent the number of classes used for categorical classification.

Table 2. The list of 36 isozyme loci usec for a comparative assessment of genetic diversity in 1,200 durum and 1,200 wild emmer wheat accessions from West Asia.

Enzyme	Usual Short Name	I.B.U. * Number
Acid phosphatase-1	Acp-1	3.1.3.2
Acid phosphatase-2	Acp-2	3.1.3.2
Acid phosphatase-3	Acp-3	3.1.3.2
Aconitate hydratase-1	Aco-1	4.2.1.3
Aconitate hydratase-2	Aco-2	4.2.1.3
Diaphorase-1	Dia-1	1.6.2.2
Diaphorase-2	Dia-2	1.6.2.2
Endopeptidase	Enp-1	3.4.22
Esterase-1	Est-1	3.1.1.1
Esterase-2	Est-2	3.1.1.1
Esterase-3	Est-3	3.1.1.1
Esterase-4	Est-4	3.1.1.1
Glucose-6-phosphate dehydrogenase-1	G-6Pd-1	1.1.1.49
Glucose-6-phosphate dehydrogenase-2	G-6Pd-2	1.1.1.49
Glutamate dehydrogenase	Gdh	1.4.1.3
Glutamic-oxaloacetic transaminase-1	Got-1	2.6.1.1
Glutamic-oxaloacetic transaminase-2	Got-2	2.6.1.1
Glutamic-oxaloacetic transaminase-3	Got-3	2.6.1.1
Hexokinase-1	Hk-1	2.7.1.1
Hexokinase-2	Hk-2	2.7.1.1
Isocitrate dehydrogenase-1	Idh-1	1.1.1.42
Isocitrate dehydrogenase-2	Idh-2	1.1.1.42
Lucine aminopeptidase	Lap-1	3.4.1.1
Malate dehydrogenase-1	Mdh-1	1.1.1.3
Malate dehydrogenase-2	Mdh-2	1.1.1.37
Malic enzyme	Me	1.1.1.40
NADH-dehydrogenase-1	Ndh-1	1.6.99.3
NADH-dehydrogenase-2	Ndh-2	1.6.99.3
Peroxide-1	per-1	1.11.1.7
Peroxide-2	per-2	1.11.1.7
Phosphoglucoisomerase-1	Pgi-1	5.3.1.9
Phosphoglucoisomerase-2	Pgi-2	5.3.1.9
Phosphoglucomutase	Pgm	2.7.5.1
6-Phosphogluconate dehydrogenase-1	Pgd-1	1.1.1.44
6-Phosphoglulconate dehydrogenase-2	Pgd-2	1.1.1.44
Shikimate dehydrogenase-1	Sdh-1	1.11.4.3

*IEC number assigned by the International Biochemistry Union, 1984

Table 3. Differences between the tolerant (T) and susceptible (S) genotypes grown under non-irrigated (NI) and irrigated (I) field conditions in 1986 and and 1987.

Year	Treatment	Genotype Group	CO_2 exchange rate $\mu mol\ m^{-2}s^{-1}$	Stomatal resistance $(s\ cm^{-1})$	Internal CO_2 (ppm)	Water use efficiency $(\mu mol\ mmol^{-1})$	Chlorophyll content $(\mu g\ cm^{-2})$	Specific Leaf Weight $(\mu g\ cm^{-2})$	Leaf area (cm^2)	Shoot dry weight (g)	Yield (g)
1986	NI †	T §	25.7	2.4	205	3.0	50.8	5.7	302	14.8	11.2
	NI	S	25.0	2.3	215	2.7	47.5	6.0	246	13.2	8.3
			ns	ns	*	*	*	ns	*	**	*
	I	T	28.9	1.9	203	3.0	51.3	5.5	506	33.9	18.3
	I	S	27.9	1.8	208	2.8	49.6	5.6	501	24.1	15.7
			ns	ns	*	ns	ns	ns	ns	ns	ns
1987	NI	T	19.5	4.9	188	4.0	50.3	5.6	431	9.3	6.7
	NI	S	18.5	5.1	205	3.6	42.6	5.7	394	6.5	4.3
			ns	ns	**	**	**	ns	*	*	*
	I	T	23.3	3.1	202	3.9	51.1	5.6	564	17.4	14.8
	I	S	22.7	3.0	213	3.7	47.5	5.6	535	13.6	10.8
			ns	ns	*	ns	*	ns	ns	ns	ns
NI vs I 1986			**	**	ns	ns	ns	ns	**	**	**
NI vs I 1987			**	**	**	ns	ns	ns	**	**	**

ns not significant

† NI=non-irrigated; I= irrigated § T= Tolerant S= susceptible

*,**Tolerant and susceptible genotypes differ significantly at the 0.05 and 0.01 probability levels respectively

** Irrigated and non-irrigated treatments differ at the 0.01 probability level.

Table 4. Product-moment correlation coefficients between rate of excised-leaf water loss (RWL) and nine physiological characters and grain yield under field conditions in Saskatoon, Canada in 1986 and 1987.

Character	Correlation coefficient (r^+) 1986	1987
Photosynthetic CO_2 exchange rate (CER)	-0.27	-0.27
Stomatal resistance (r_s)	-0.27	-0.17
Internal CO_2 concentration (INCO2)	0.50*	0.72**
Water-use efficiency (WUE)	-0.79**	-0.46*
Chlorophyll a + b content (Chl)	-0.44*	-0.63**
Specific leaf weight (SLW)	0.29	0.23
Leaf water content (LWC)	-0.70**	-0.89**
Total leaf area (LA)	-0.22	-0.66**
Shoot dry weight (SDW)	-0.67**	-0.70**
Grain yield per plant	-0.62**	-0.62**

$^+$r calculated from 20 genlotype means for each trait.

*,** r significant at the 0.05 and 0.01 probability levels, respectively.

Table 5. Mean grain yields (g m^{-2}) of durum wheats with high and low rates of excised-leaf water loss at Swift Current and Saskatoon, Canada in 1985 through 1987, and at Tel Hadya, Breda, and Bouider, Syria in 1985-86.

Location	Year	Local checks		Canadian checks		high water loss genotypes		low water loss genotypes		Probability**
		Mean	SE*	Mean	SE	Mean	SE	Mean	SE	
Swift Current	1985	55.1	4.9	-		20.1	1.7	50.2	2.7	0.0001
	1986	212.5	12.5	-		161.5	5.2	165.1	5.7	0.6837
Saskatoon	1985	181.6	21.5	-		109.3	7.4	147.5	11.6	0.0152
Rainfed	1986	248.0	17.7	-		188.6	5.9	179.5	6.7	0.3037
Irrigated	1986	389.2	23.4	-		214.2	7.4	205.4	9.3	0.4625
	1987	102.9	9.3	-		78.8	2.7	111.6	4.2	0.0001
Tel Hadya	1985-86	313.1	16.5	245.2	16.5	237.1	13.3	257.4	18.8	0.3829
Breda	1985-86	82.1	3.4	90.4	4.8	93.5	4.4	105.6	6.0	0.1091
Bouider	1985-86	35.3	1.5	23.9	2.5	23.4	1.9	32.7	3.4	0.0308

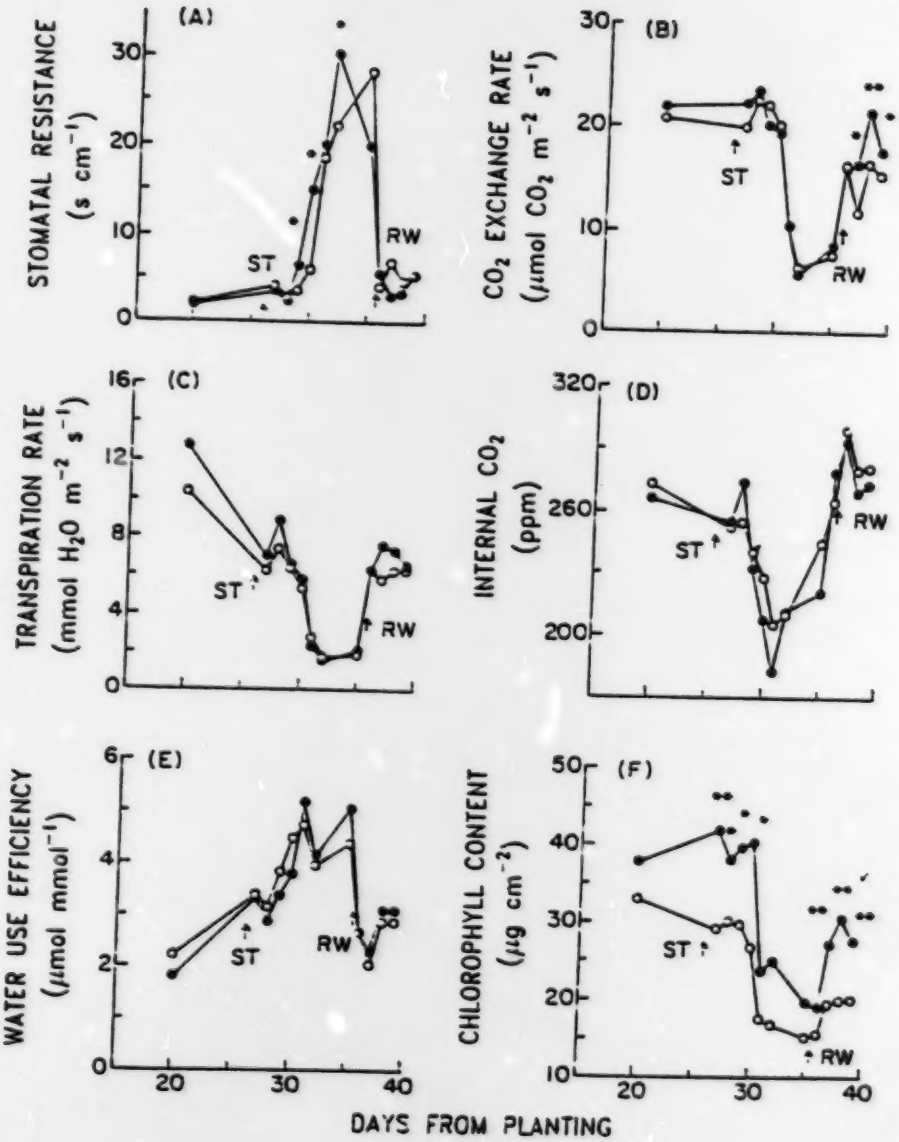
* Standard error of the mean.

** Probability of Type I error for the null hypothesis that the yields of the high and low groups are not different.

Table 6. Estimates of overall genetic diversity (H) and polymorphic index (Pi) for 36 isozyme loci in durum and wild emmer wheat accessions from West Asia.

Species	Shannon's information index (H)	Polymorphic index (Pi)	Number of of random accessions
Durum wheat (**Triticum turgidum** var. **Durum**)	1.093	0.663	1,200
Wild emmer wheat (**Triticum** var. **Dicoccoides**)	1.318	0.788	1,200

Figure 1. Effect of water treatment on means of physiological characters in drought tolerant (●) and susceptible (○) genotypes in experiment 2. (* and ** indicate significant differences between tolerant and susceptible means within a measurement day at the 5% and 1% level respectively). Arrows indicate initiation of stress (ST) or rewatering (RW) periods.


(A)
STOMATAL RESISTANCE (s cm⁻¹)
ST
RW
(B)
CO2 EXCHANGE RATE (μmol CO2 m⁻² s⁻¹)
ST
RW
(C)
TRANSPIRATION RATE (mmol H2O m⁻² s⁻¹)
ST
RW
(D)
INTERNAL CO2 (ppm)
ST
RW
(E)
WATER USE EFFICIENCY (μmol mmol⁻¹)
ST
RW
(F)
CHLOROPHYLL CONTENT (μg cm⁻²)
ST
RW
DAYS FROM PLANTING